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# Geographical variation in dormancy in a copepod: evidence from population crosses

Grace A. Wyngaard
*Department of Biology, James Madison University, Harrisonburg, Virginia 22807, USA*

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## Abstract

Populations of the freshwater copepod *Mesocyclops edax* inhabiting Michigan lakes are dormant during winter, whereas populations inhabiting Florida lakes develop and reproduce continuously throughout the year. A Michigan and a Florida population were exposed to dormancy inducing conditions (low temperature and short photoperiod) in the laboratory and observed for indications of dormancy. All Michigan individuals and a small percentage of the Florida individuals entered dormancy as indicated by prolonged duration of the fourth copepodid instar and cessation of feeding. I suggest that in these population these observations represent diapause, rather than quiescence. The two populations were crossbred to examine the nature of inheritance of dormancy. The $F_1$ hybrids exhibited an incidence of diapause approximately intermediate between the Florida and Michigan parental stocks. The backcrosses of $F_1$ individuals to the Michigan and Florida stocks, respectively, exhibited a high and an intermediate incidence of diapause. Survival of the $F_2$ crosses was very low. The present study presents evidence of genetic differentiation between the Michigan and Florida populations of *M. edax* with respect to ability to diapause.

## Introduction

Although dormancy occurs in numerous freshwater cyclopoid copepods and has profound consequences on the life cycle, it is difficult to define precisely. The most clearly articulated definitions of dormancy are gleaned from the extensive studies of terrestrial insects (reviews by Tauber *et al.*, 1986; Danks, 1987). Danks (1987: p 8) broadly defined dormancy as a 'state of suppressed development' which represents either quiescence or diapause. Danks (1987: p 18) defined quiescence as 'an immediate direct response to a limiting factor, such as cessation of development if temperatures fall below the developmental threshold but immediate resumption of development if they rise above it.' He defined diapause as 'a more profound interruption that routes the metabolic programme of the organisms away from direct developmental pathways and into a much more clearly organized break in development that is not controlled simply by the direct action of environmental factors, and which in nature precedes the advent of adverse conditions.'

Characteristics of dormancy in cyclopoids include prolonged duration of juvenile instars (Smyly, 1962), cessation of feeding (Williamson, 1984), settlement to the bottom muds (Elgmork, 1962), encystment (Cole, 1953), and reduced oxygen consumption (Watson & Smallman, 1971a). Most studies of dormancy in cyclopoids have not attempted to distinguish quiescence from diapause. These two forms of dormancy are sometimes confused with one another, which can lead to problems in interpretation of life histories, as Grice and Marcus (1981) have discussed using the example of dormant eggs of marine calanoid copepods. In the absence of definitive knowledge of the similarity of dormancy between insects and copepods, I have chosen to adopt the definitions most frequently employed in studies of insects as a starting point in thinking about and studying dormancy in copepods.

Diapause is a more complicated developmental process and represents a greater committment on the part of an organism to a particular physiological state than quiescence. For this reason variation in the presence or timing of diapause among conspecific populations may reflect selection pressures under which the populations have evolved and provide insights into how populations have adapted to their respective local environments. Diapause has been shown to be important fitness component and to evolve rapidly in one species of calanoid copepod (Hairston & Walton, 1986).

In the present study I use common rearing techniques and laboratory induction of dormancy to compare the percentage of dormant individuals in Michigan and Florida populations of the widely distributed freshwater copepod *Mesocyclops edax* (S. A. Forbes). Individuals inhabiting Michigan lakes undergo two continuously developing and reproductive summer generations and a third that is dormant during winter (Wyngaard, unpub. data), but individuals inhabiting Florida lakes develop and reproduce continuously throughout the year (Wyngaard *et al.*, 1982). These two populations are different genetically with respect to maturation time, body size, clutch size, and egg size (Allan, 1984; Wyngaard, 1986). This study attempts to determine if they differ in the ability to enter dormancy and whether they exhibit quiescence or diapause. Hybrid crosses are used to provide information on the nature of the inheritance of this trait.

## Materials and methods

*Study site and organism* – Ovigerous females were collected from Lake Thonotosassa in Hillsborough Co., Florida and from Douglas Lake in Cheybogan Co., Michigan during June 1986, a time when cues that might stimulate dormancy in the lake population were likely to be absent. The lakes and populations are described by Wyngaard (1986) and Dawes *et al.* (1987, and references therein). The life cycle of *M. edax* consists of an egg, six naupliar (larval) instars (I–VI), five copepodid (juvenile) instars (I–V) and an adult (VI) which does not molt.

*Laboratory studies* – Offspring of the 78 and 53 field collected Michigan and Florida females, respectively, were reared individually to adulthood for a acclimation generation ($G_1$) under identical conditions at 25 ± 0.5 °C, 14 h light: 10 h dark and light intensity of approximately 45–50 $uM^{-2}s$. General Electric cool white fluorescent bulbs were used. Culture methods described by Wyngaard (1986) were used, except that copepodids were fed newly hatched *Artemia salina* nauplii. The $G_1$ adults were mated randomly to yield the following crosses: Michigan x Michigan ($P_m$), Florida x Florida ($P_f$), and Michigan x Florida ($F_1$). The $F_1$ adults were mated to each other to yield $F_2$ hybrids, and also to the parental lines to yield backcrosses to the Michigan ($F_1 \times P_m$) and the Florida ($F_1 \times P_f$) lines. Reciprocal matings were performed for each type of cross. The animals derived from each cross in the present study were chosen haphazardly from families reared from crossbreedings in another study (Wyngaard, in prep). The number of families sampled from each type of cross ranged between 9 and 83. The number of offspring per family ranged from one to five.

The dormancy inducing treatment consisted of placing nauplius IV, V, and VI instars into 10 ± 0.5 °C, 8 h light: 16 h dark, and

18–36 uM$^{-2}$s. Animals remained under these conditions until they matured. A previous study (Bishop-Rayle, 1988) compared individuals of *M. edax* exposed to the aforementioned dormancy inducing conditions during different instars and revealed that exposure during the copepodid I instar to the these cues stimulated dormancy. Exposure of copepodid II–IV instars to these cues did not stimulate dormancy. Individuals were observed and offered *Artemia salina* nauplii every few days. Individuals that spent more than 60 d in a single instar and did not eat *Artemia salina* nauplii were considered dormant.

Twenty copepodid IV instars, each of which spent longer than 70 d but less than 99 d in the copepodid IV instar and did not feed, were removed from 10 °C and 8 h light: 16 h dark conditions and transferred to 25 °C and 14 h light: 10 h dark in an effort to terminate dormancy. One sib of each of these twenty instars were maintained in the dormancy inducing treatment. Individuals were observed twice daily for molting and feeding. These twenty individuals were excluded from the data described in Fig. 1 and Table 1 in order to avoid a bias in the estimates of duration of the copepodid IV instar and survivorship to adulthood. Yates correction was used in each calculation of the G liklihood test (Sokal & Rohlf, 1969).

## Results

The duration of the juvenile copepodid instars ranged from 5 to 45 d and the distributions were unimodal with the exception of the copepodid IV instar (Fig. 1). The copepodid IV instar comprised two separate groups of individuals, one with the durations of the other four instars and one with prolonged durations ranging from 60 to 115 d. This pattern was consistent for all crosses. Individuals that spent more than 60 d in the copepodid IV instar did not feed upon *Artemia* nauplii, whereas those that spent less than 60 in the copepodid IV instar did feed. Two females, one in each of the backcrosses to the Michigan and Florida parental lines, were the only females that did not feed. Both spent less than 60 d in the copepodid IV instar and fed during this instar. Thus, based upon the criteria of prolonged duration of instar and cessation of feeding, all individuals that entered dormancy did so as copepodid IV instars. Sex ratios (females: males) of animals that were dormant were 1 : 1 in the Michigan parental line and the combined backcrosses. Sex

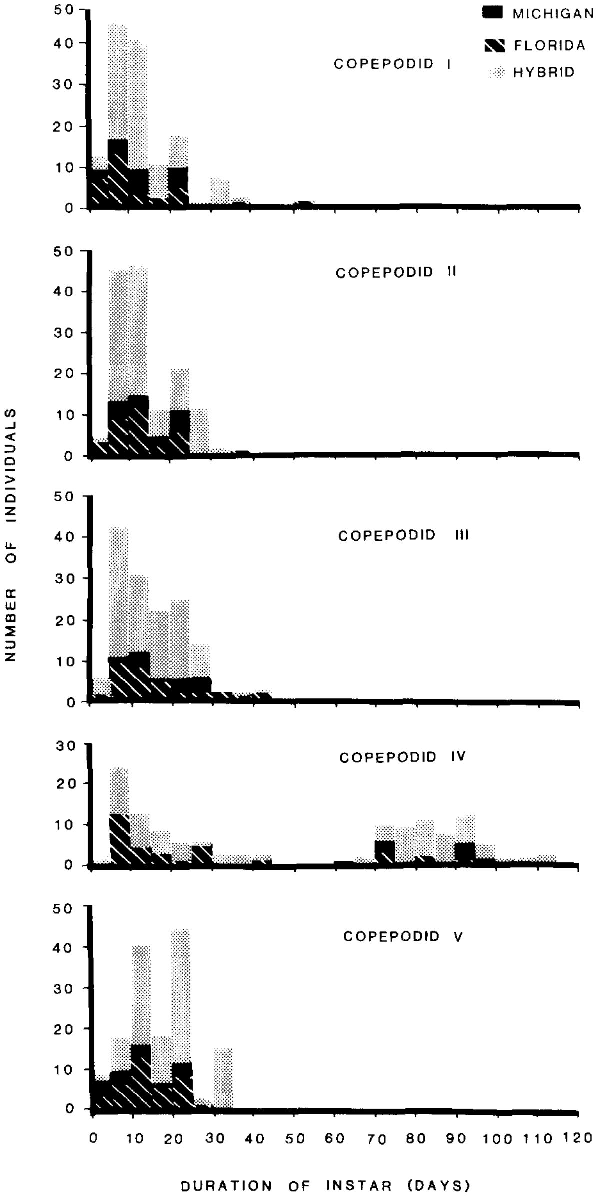

*Fig. 1.* Duration of copepodid I, II, III, IV, and V instars of Michigan and Florida *Mesocyclops edax* and their hybrids reared at 10 °C and 8 h light: 16 h dark.

*Table 1.* Incidence of dormancy of copepodid IV instars and survival to adult in parental lines and hybrid crosses of Michigan and Florida populations of *Mesocyclops edax* reared at 10 °C and 8 h light: 16 h dark. Numbers in parentheses refer to number of animals that survived to adulthood in each cross on which percentage of dormant individuals is based.

| | $P_m$ | $F_1$ | $P_f$ | $F_1 \times P_m$ | $F_1 \times P_f$ | $F_2$ |
|---|---|---|---|---|---|---|
| % Diapause | 100<br>(14) | 41.0<br>(39) | 16.2<br>(37) | 92.8<br>(28) | 41.7<br>(36) | 50.0<br>(2) |
| No. families* | 9 | 36 | 29 | 83 | 61 | 26 |
| No. surviving families | 8 | 14 | 16 | 19 | 26 | 2 |
| % Survival to adult | 60.9 | 36.0 | 52.9 | 33.4 | 34.9 | 7.7 |
| Nauplii** | 23 | 112 | 70 | 83 | 103 | 26 |

* Number of families used to initiate each type of cross.

** Total number of nauplii placed into dormancy inducing conditions on which survival to adult is based.

ratio in the $F_1$ hybrids (1 : 3) and in the Florida parental line (1.6 : 1) contained cell frequencies of less than five individuals, making statistical comparisons between ratios inappropriate.

The percentage of dormant individuals in the Michigan parental line (100%) was significantly higher than that in the Florida parental line (16.2%) (Table 1) ($G_{(1\ df)} = 24.08, p < .005$). The Florida parental line consisted of families in which all sibs either were dormant or not with the exception of one family. This family was comprised of two males which entered dormancy in the copepodid IV instar and two females which spent their longest duration (45 d) of all instars in the copepodid III instar and fed as adults.

No significant effect of origin (Michigan or Florida) of either parent was found for percentage of individuals that entered dormancy in the $F_1$ hybrids (Fisher's exact test, $p = .028$), so the reciprocal crosses were pooled. The frequency of dormancy of $F_1$ hybrids was 41.0%. The backcrosses of the $F_1$'s to the Michigan and Florida parental lines, respectively, exhibited high and intermediate percentages of dormancy. The low survivorship of the $F_2$ hybrids in this cross yields insufficient data to describe, with confidence, the percentage of dormancy.

Survival to adulthood of the Michigan parental line was greater than that in the Florida line (Table 1) ($G_{(1\ df)} = 17.86$, $p < .005$). Individuals in each parental line survived better than individuals in the $F_1$ hybrids or backcrosses (G likelihood test, $p < 0.05$).

After a period of 60 to 115 d all of the dormant copepodid IV instars depicted in Figure 1 terminated dormancy spontaneously, began to feed, and molted to copepodid V instars without an overt, external, dormancy-terminating cue. Of the 20 copepodid IV instars removed from dormancy inducing conditions and exposed to high temperature and long daylength, 8 died and 12 molted into copepodid V instars. Individuals commenced feeding one and five days after exposure to these conditions, after which they molted to adults, yielding five females and seven males. Of these adults one mating between Florida individuals resulted in a clutch of 25 eggs.

## Discussion

Michigan and Florida populations of *M. edax* have characteristics of diapause in the laboratory, which lends support to the view that both populations are capable of entering diapause. That the trait observed in the present study is diapause, and not quiescence or torpor, is supported by the copepodid IV instar existing for a prolonged duration and ceasing to feed, two traits that occurred in response to a cue that is received in the copepodid I instar. Also the bimodal distribution of development time for copepodid IV instars suggests a different physiological condition for the two groups. A sustained, low metabolic state is implied by these observations. However, measurements of physiological attributes such as oxygen consumption and examination of physiological states using metabolic inhibitors are important and necessary in order to verify the reduction in metabolic rate.

In the present study both diapausing and nondiapausing individuals swam. Swimming has been reported in a laboratory population of diapausing *Diacyclops navus* which exhibited prolonged duration of the copepodid IV instar (Watson & Smallman, 1971a), reduced oxygen consumption, and lack of sensitivity to metabolic inhibitors in response to a cue of short day and low temperature that preceded the copepodid IV instar (Watson & Smallman, 1971b). Swimming also was observed in copepodid IV instars of a Virginia population of *M. edax* that were collected in plankton traps placed in the muds during winter (Bishop-Rayle, 1988). These instars did not feed or molt for a period of about two months after they were brought into the laboratory and maintained at 10 °C and 8 h daylength. Similarly, Williamson (1984) observed swimming and absence of feeding in numerous collections of *M. edax* collected from the sediments during winter in New Hampshire lake. These animals exhibited an increased propensity to feed as the time of spring emergence neared. Fifth stage copepodids of *Cyclops bohater*, presumed to be in diapause, actively burrowed in the laboratory when presented with mud and moved when they were touched by a pipette (Wierzbicka, 1962). Elgmork (1962) observed copepodid II–V instars of *Cyclops scutifer* collected from the sediments in winter to swim minutes after disturbing the muds, and later (Elgmork, 1980: p 412) termed this 'active diapause' which he regarded as an evolutionary step to diapause and inactivity. Most of these laboratory and field collected populations comprised only one or two instars (typically copepodid IV or V) and suggest that a cue had stimulated suppression of development at a particular instar. Except for those populations of cylcopoids that encyst during diapause, there are no direct observations to my knowledge on the swimming or burrowing activity of nonencysted cyclopoids in lake sediments. Diapausing cyclopoids that do not encyst have been assumed to be immobile, as the term resting stage implies, and thus reports of swimming in diapausing cyclopoids are problematical.

The present laboratory study corroborates reports that *M. edax* diapauses primarily as copepodid IV instars (Comita, 1972; Stucke, 1981). No adult females in the Michigan and Florida lines were determined to be in diapause when the criterion of absence of feeding was used. Bishop-Rayle (1988) examined the incidence of diapause in forty nine putatively unrelated families of a Virginia population of *M. edax* and found that five percent of the individuals did not feed as adult females despite being given feeding trials for two months. It is impossible to use the criterion of prolonged duration of instars to ascertain diapause in adult females which do not molt. No insect populations are known to diapause as both juveniles and adults (Tauber *et al.*, 1986; Danks, 1987). If cyclopoid diapause is equivalent to insect diapause, one might speculate that the adult females were quiescent. Cole (1953) found adult females in the sediments during winter in a Minnesota lake, as did Williamson (1984) in New Hampshire, Elgmork (Univ. of Oslo, pers. comm.) in Connecticut, and Bishop-Rayle (1988) in Virginia.

Diapausing individuals of *M. edax* which remained under short day and low temperature conditions spontaneously molted to the copepodid V instar and commenced feeding despite the absence of an apparent cue. This behavior has been noted also in diapausing *Cyclops strenuus* (Smyly, 1962). Some insect populations also terminate diapause without a cue (Danks, 1987). Because the appearance of individuals in the plankton in spring after absence during winter seems to occur within a span of days or a few weeks (Comita, 1972; Stucke, 1981; Bishop-Rayle, 1988), it seems reasonable to argue that some environmental cue may contribute to timing of termination. If cyclopoids leave the sediments and enter the water column in response to increasing temperatures and favorable oxygen conditions as shown by Papinska (1984), these physical factors may contribute to an apparent synchronized appearance in the plankton in the spring. Additionally, genetically based differences in duration of diapause among individuals that enter diapause at different times of the season may contribute to synchronization of emergence from diapause, as argued by Marcus (1987) using both laboratory and field populations of *Labidocera aestiva.*

The Michigan and Florida populations differ with respect to percentage of the population that is capable of initiating diapause in response to the cues offered in this study. It is difficult to relate these findings to the natural populations, because of the paucity of information on characteristics of diapause in field populations, the physical environment, and environmental factors which serve as cues to initiate and terminate diapause in these populations. Several aspects of the biology of the field populations are known. No evidence of diapause, as characterized by prolonged duration of an instar, cessation of feeding, or lack of reproduction in winter collected Florida individuals that were brought into the laboratory for either determinations of egg duration rate (Wyngaard, 1978) or life table analyses (Wyngaard, 1986) were observed. Reproduction nearly ceases in the lake when temperatures decline to 12 °C (Wyngaard *et al.*, 1982); however, all developmental instars are present in the plankton throughout the year. The Michigan *M. edax* disappear from the water column at the end of October, and reappear as late stage copepodids and adults in the water column in June (pers. obs.). The winter temperatures drop well below 10 °C in the Michigan lake which is covered with ice during the entire winter.

If photoperiod, or rate of change in photoperiod modified by temperature, are the cues that induce diapause, then the cues that elicit the highest percentage of diapausing individuals might differ between the Michigan and Florida populations. Photoperiodic cues for diapause have been shown to differ among latitudinally separated populations (Marcus, 1984) and among local populations with differing phenologies (Hairston & Olds, 1986). The stikingly different percentages of diapausing individuals between the Michigan and Florida populations revealed in the present study suggest that these populations have differentiated genetically with respect to be ability to diapause. What is most interesting is the observation that a small proportion of the Florida population is capable of a diapause. These results are similar to those of Marcus (1984) who reported differences in genetic capacity to diapause in several latitudinally separated populations of the marine calanoid *Labidocera aestiva.* Speculation on why genes conferring the ability to diapause are present in the Florida population and the phylogenetic origin of diapause in the *Mesocyclops* group is beyond the scope of the present study.

Many cases of polygenic inheritance of diapause in insects have been reported (Tauber *et al.*, 1986). However, other modes of inheritance also have been reported in insects (Tauber *et al.*, 1986). More study on the nature of the inheritance of diapause is needed to determine if copepods and insects are similar in this respect. No statistically significant effect of dominance was detected in the $F_1$ hybrids, although the sample size was small. Family size was small in the present study, so variation in presence or absence of diapause within a family could not be examined. Bishop-Rayle (1988) reported that 48 of 49 families of a Virginia population of *M. edax* contained both diapausing and nondiapausing sibs.

The poor survival of the hybrids, particularly the $F_2$ hybrids, relative to the parental lines, and the lower incidence of diapause in the $F_1$ hybrids relative to the Michigan parental line are additional evidence of genetic differentiation in these populations with respect to traits that influence fitness. Whether this would occur also between crosses of local populations, seems less likely (Watson, 1986). A larger crossbreeding study of Michigan and Florida animals reared at 25 °C and low and high food levels also revealed poor survival of $F_2$'s (ms in prep). These findings may reflect incipient speciation in the Michigan and

Florida populations and suggest that the Michigan and Florida genomes do not integrate well with one another.

The ultimate cause of diapause in these populations of *M. edax* is not known, although temperature may be a factor in this warm-water genus. Survival in *M. edax* is strongly affected by temperature, decreasing from 97% at 25 °C to about 50% at 15 °C (Wyngaard, 1986) and 10 °C (present study, Bishop-Rayle, 1988). Danks (1977) reported that cold-hardiness is not necessarily associated with diapause, so stress attributable to cold may not be the correct explanation. Low oxygen levels have been suggested as a causative factor of diapause in some freshwater cyclopoids (Wierzbicka, 1962). Strickler & Twombly (1975) argued that diapause in cyclopoids most probably evolved as a response to avoid predation, as copepods could more easily compensate for adverse physical conditions with simpler adaptive responses. Some evidence exists suggesting that fish predation influences the likelihood that cyclopoids will diapause (Nilssen, 1977) and that interactions of fish predation and low food levels select for diapause in the cyclopoid *Cyclops abyssorum* in alpine lakes in Poland (Papinska, 1987). Hairston & Munns (1984) convincingly depicted the effects of predation on timing of production of diapausing eggs in a freshwater calanoid. Together these point to biotic factors as an important area in which to focus investigations of the evolution of diapause in zooplankton. The influence of the biotic and abiotic environments are obviously intertwined as the causative factors of diapause. Explanations of variation among populations in incidence or phenology of diapause will likely necessitate understanding the relationships of factors such as predation, competition, temperature, photoperiod, and oxygen to the life cycles of copepods.

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